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A new species of paper wasp from the genus *Ropalidia* Guérin-Méneville from South Africa (Hymenoptera, Vespidae)

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Abstract

Ropalidia amabala **sp. nov.** is described and compared to the known African species of this genus. In addition, the nest and nesting habits are described. This species demonstrates the nesting pattern previously recorded only in Madagascar, which includes nesting directly on a tree trunk and using lichen as the nest-building source material to blend in with the surrounding lichen patches. In contrast to the Malagasy species, which clean the nesting area of lichen, this new South African species constructs the nest in a clear area of the trunk between patches of lichen. This provides excellent visual concealment of the nest and suggests that visually driven predators are the primary selective factor. The morphology for both sexes of this species disagrees with known Malagasy species, suggesting that they are separate evolutionary lineages and hence that this nesting behaviour evolved independently.

Keywords

Afrotropical, identification key, new species, social wasps, taxonomy

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Introduction

The recent revision of the social wasps of the genus *Ropalidia* Guerin-Méneville established 48 valid mainland African species (Polašek et al. 2022). The greatest species richness was recorded along the Indian Ocean coast, with a decline towards the western parts of Africa. Numerous small and isolated populations were encountered, sometimes with a high degree of sub-structuring in the population of a single species. Two large groups of mainland species were established: the *capensis* and the non-*capensis* group (Polašek et al. 2022). In addition to several morphological differences (clavate antenna in females, elevated tyloids above the flagellomere surface and the tarsal spur of the fore leg in males present in the *capensis*-group and absent in the non-*capensis* group), these groups exhibited strong genetic divergence; interestingly, the inclusion of several Malagasy *Ropalidia* suggested that the *capensis* group is genetically closer to the Malagasy species (Polašek et al. 2022). The same study already suggested the existence of additional species, based on the observational data from the citizen-science platform iNaturalist (www.inaturalist.org). An undescribed taxon was observed in South Africa, suggesting an interesting colour pattern not previously recorded in any known species (Polašek et al. 2022).

The genus *Ropalidia* Guerin-Méneville exhibits the greatest diversity of nesting architecture among the Old World Polistinae (Wenzel 1998). The majority of the Malagasy *Ropalidia* species each have a unique nest architecture (Blommers 2012), suggesting that the evolutionary pressure is strongly exerted in their nesting behaviour, which contributes to the speciation process. In contrast, the mainland African species exhibit a minimal nest architecture diversity (Polašek et al. 2022). In most cases, the nest is discoid, located on branches or anthropogenic objects, suggesting that evolutionary pressure and the subsequent speciation process is disassociated with the nesting habits of mainland African species.

Materials and methods

This study is based on the examination of specimens from the Albany Museum (**AMGS**) in Makhanda, South Africa, which were not included in the original revision (Polašek et al. 2022). The study was also supplemented by the field observation of one wasp colony that was later collected and included in the type series. In addition, the nest, adult wasps and all of the larvae were collected and preserved in ethanol. Finally, we also performed a careful analysis of the neighbouring geographical region in iNaturalist, aiming to identify any possible observation of this taxon. The examined specimens are deposited in three institutions, the Albany Museum, Makhanda (AMGS), American Museum of Natural History (**AMNH**) and Iziko South African Museum, Cape Town (**SAMC**).

Morphological features used in species description include the upes (upper portion of the lateral arm of epistomal suture) and the oculo-clypeal angle, the highest position where the lateral margin of the clypeus touches the eye; this angle is also the lowest point of the inner orbit area. Two additional characteristics from the propodeum were

used: the superior carina (which is present in the upper part of the propodeum, just under the metanotum); and the inferior propodeal carina (located more distally, lateral and slightly superior to the valvula).

The specimen analysis was based on a comparison with known African species, including the specimens from Madagascar, obtained through loans from the Oberösterreichisches Landesmuseum, Linz, Austria, National Museum of Natural History, Naturalis, Leiden, the Netherlands, Museo di Storia Naturale di Venezia, Italy and Entomological Collection, ETH Zurich, Switzerland (details provided in the acknowledgements). Specimens were photographed using a Leica S9i with an integrated camera. Images were stacked using *Helicon Focus* 6.8.0 software (Helicon Soft, Kharkiv, Ukraine; https://www.heliconsoft.com).

Results

Ropalidia amabala **Polašek, Bellingan & van Noort, sp. nov.**
http://zoobank.org/D2F40851-7892-4C82-AA17-20C1D462BF72

Type specimens. ***Holotype*****:** Oatlands Road, Grahamstown, 33°18'16.13S, 26°31'26.62E, South Africa, Nov 2020, leg TA Bellingan and MH Villet, 1♀. (AMGS). ***Paratypes*** [10♀♀, 3♂♂]: 9♀♀ and 1♂ with the same location data as the holotype (including series of larva in ethanol and a nest) (AMGS, AMNH, SAMC); Kenton on Sea, South Africa, January 1972, leg RA Jubb (malaise trap), 2♂♂ (AMGS); Howison's Poort, Grahamstown, South Africa, 14–29.II.1972, leg FW Gess, 1♀ (AMGS). The total number of examined specimens: 11♀♀, 3♂♂. Observational data: Mount Michael, Hilton, -29.575806, 30.288814, South Africa, 1♀, 1♂; obs. happyasacupcake (https://www.inaturalist.org/observations/20355582).

Diagnosis. This species can easily be separated from other African mainland species by the dark brown ground colour with a reddish hue, combined with a large whitish-yellow area on the pronotum, and a posterior band on T2 that is merged with six semi-circular spots. The circular location of these accessory spots is a sufficient criterion for a unique species determination, since other mainland *Ropalidia* do not have a central ventral or dorsal spot on T2 or S2. In addition, males have an interesting pattern of clypeus punctation, characterised by the presence of large and dense punctations in the basal half, while the apical half of clypeus is almost entirely impunctate.

Description. Females. Wing length 8.6–9.7 mm. ***Colour.*** The ground colour is dark brown with a reddish tone (Fig. 1a). Clypeus with the basal two thirds in ground colour, the apical third is whitish-yellow; sometimes, suffused whitish-yellow markings can appear under the upes (Fig. 1b). Interantennal area sometimes with whitish-yellow spot, commonly without any markings. Mandible with a yellowish antero-basal spot (Fig. 1b), gena and tempora brown-reddish, lighter than the ground colour (Fig. 1a). The antennal scape blackened dorsally, with a brown underside (Fig. 1a). AF1 is similarly coloured to *R. tenebrica* Polašek, 2022, with a brown base and a distal blackening. The remaining flagellomeres are black dorsally, occasionally brownish

ventrally. The pronotum is mainly whitish-yellow, with only the basal colour remaining at the posterior (mesopleural) margin and inferior angle (Fig. 1a). Mesosoma in the ground colour, posterior margins of scutellum and metanotum brownish (Fig. 1c). Propodeum and the rest of the mesosoma in ground colour (occasionally a minute yellowish spot at the tip of coxa I). Femora in the ground colour, tibia brownish, lighter than the femur (Fig. 1a). The apical spot of the fore wing is dark and opaque, nervature brown, stigma dark brown and opaque (Fig. 1a). Metasoma basally with the ground colour (more distal segments can be brownish). T1 without any markings, T2 with a thick posterior band and six merged semi-circular spots (Fig. 1a); these spots are arranged unevenly, one dorsally, one ventrally and two on each side (Fig. 1a, d). T2 lamella is yellowish, comparatively shorter.

Head. Clypeus wide, about 1.4 times wider than long, with a moderately convex surface; the basal part, in ground colour, is covered by shallow and large punctations, which lose contour apically and convert to poorly defined craters in the yellow areas of the clypeus (Fig. 1b). The upes is straight and comparatively longer, while the juxtamandibular notch is shallow; the oculo-clypeal angle is not sharp (Fig. 1b). The general appearance of the clypeus mostly resembles *R. excavata* Giordani Soika, 1977 females, but with a less developed juxtamandibular notch. The entire clypeal surface is covered by a golden under-layer of pubescence and stronger yellowish protruding setae of approximately equal length basally and apically. Gena is slightly narrower than the broadest part of the eye, most commonly about 0.9 times its width (Fig. 1a). It is covered by large and well-defined punctums next to the eye margin, smaller and shallower close to the occipital carina. Frons is covered by large and coarse punctation, extending until the ocelli; it dissipates posteriorly towards the occipital carina. The occipital carina is complete and slightly sinuate. The complex eye is covered by short and sparse setae. The ocellar triangle is barely acute forward or equilateral. Frons is covered by yellowish straight or slightly bent setae, which are about as long as the forward ocellus diameter. The scape is barely shorter than AF1; AF2 is about as wide as long.

Mesosoma. Mesosoma covered by comparatively denser and coarser punctation, similar to *R. excavata* Giordani Soika, 1977. Punctation of mesonotum is of equal density throughout, including the areas lateral to parapsidal furrows. The pronotum is densely punctated, but punctation is well defined only in the remaining dark areas; punctation on the whitish-yellow areas is comparatively shallower and less defined. Mesopleura covered by large and coarse punctums, while those on the metapleura are

Figure 1. *Ropalidia amabala* sp. nov., female **a** habitus **b** head **c** scutellum, metanotum and propodeum **d** T2, dorsally.

about half their size and less dense. The scutellum is comparatively more developed and elevated, similar to *R. soikai* Polašek & Kehinde, in contrast to the more flattened scutellum in *R. excavata* Giordani Soika, 1977 (Fig. 1c). The median carina of the scutellum is barely visible in the anterior part, while it is completely lacking dorsally, thus resembling the entire *nigrofemorata* group of species. The metanotum is posteriorly flattened, with a moderate size of the shiny impunctate area. The propodeal excavation is comparatively shallower, with well-developed superior carina, variable striations (more or less developed, but always visible), and variably developed inferior carina (Fig. 1c). The general appearance of the propodeum mostly resembles *R. kuficha* Polašek, 2022, which has only thin yellow markings on the body.

Metasoma. Tergum 1 is pyriform and slightly elongate, similar to *R. guttatipennis* (de Saussure), with more developed punctation on the posterior half. T2 is covered by dense directional punctation, which is sparse on S2. The entire T2 surface is covered by short yellowish protruding setae, which barely extend posteriorly over the lamella.

Males resemble females, except having more yellowish markings on the face and the ventral side of the mesosoma. Wing length 8.2–9.3 mm. ***Colour.*** Most of the face is yellowish-white, except dark-brown frons (Fig. 2a). Tempora with a reddish line, gena with a yellow widened area close to the eye, posteriorly in ground colour. Antenna dorsally black; scape yellow underneath, flagellomeres orange (Fig. 2a). Pronotum with a larger whitish-yellow area, scutellum and postscutellum posteriorly with a faint reddish area. Mesopleura anteriorly with a large yellow patch, laterally without yellow markings. Coxa I and II, and femora I and II ventrally entirely yellow (Fig. 2b). Tibia and tarsi brown, in contrast to dark-brown (ground colour) dorsal side of the femora, similarly to *R. nigrofemorata* (Cameron). Wings translucent, with minimal anterior yellowing close to stigma; nervature brown, stigma dark brown and opaque. The apical spot is well developed, faintly reaching stigma (equal to Fig. 1a). Metasoma in the ground colour, except a faint reddish posterior band on T1 and a characteristic whitish-yellow posterior band on T2 and S2, with integrated six spots (Fig. 2b).

Head. The clypeus is broader than long (1.3 times), with a flattened surface, which is minimally depressed sub-apically in some specimens (Fig. 2a). The clypeus is similar

Figure 2. *Ropalidia amabala* sp. nov., male **a** head **b** habitus, inferior oblique view **c** antenna, dorsally.

to *R. nigrofemorata* (Cameron), with evenly curved upes, long and straight basal notch, lacking the oculo-clypeal angle and a barely projecting, subacute apex (Fig. 2a). Clypeus base is covered by large and shallow punctums, which become less defined apically; the apical third of the clypeus surface is usually completely impunctate (Fig. 2a). Frons covered by large and coarse punctation, which becomes smaller on tempora, but then reverts to equally large punctum size on gena, close to the eye; punctums on tempora and gena posteriorly become somewhat smaller and less defined. Gena about 0.4–0.5 times the eye width. Mandibles shiny, nearly impunctate; only a few basal punctums can be more defined. Scape broadened, about 1.6–1.9 times the AF1 base width, shorter than AF1; AF2 about 1.4–1.6 times longer than wide. Tyloids are weak and thin, and they are not elevated above the flagellomere surface; the first one originates on the distal part of AF1, as a thin line that gradually emerges and becomes discernible of the distal half of the flagellomere length. Those on AF2 and AF3 are linear and thin, gradually widening on AF4 and AF5 and reaching about a half of the inner flagellomere surface in more distal segments, or a majority of surface in the terminal flagellomere (Fig. 2c). In all instances, their surface is partly shiny but less than in *R. nigrofemorata* (Cameron). The terminal flagellomere is elongated, about 1.7 times the AF10, with a rounded tip (Fig. 2c).

Mesosoma. Fore tarsal spur 1 not developed.

Metasoma. S7 is flattened or weakly concave (Fig. 2b).

Key to species update

The key provided in the previous genus revision (Polašek et al. 2022) should be updated with the following elements.

Females

35a Basal body colour dark brown with a reddish hue, with a large whitish-yellow area on the pronotum and six whitish-yellow spots integrated with a posterior band on T2 and S2 (Fig. 1a). The apical spot of the fore wing is dark, but faintly extending towards the stigma (Fig. 1a). The median carina of the scutellum is weakly developed, barely visible dorsally. South Africa..... .....***R. amabala* sp. nov.**

– Basal body colour pattern is different; if the pronotum and T2 have large markings, these are yellow, and the basal body colour is brown or ferruginous (rarely, specimens of *R. aethiopica* may have yellowish markings or even reddish basal colour, but in these cases, the median scutellar carina is well developed dorsally) **35**

Males

18a Basal body colour dark brown with a reddish hue, with a large whitish-yellow area on the pronotum and six whitish-yellow spots integrated with a posterior band on T2 and S2 (Fig. 1a). The apical spot of the fore wing is dark, but faintly

extending towards the stigma (Fig. 1a). The median carina of the scutellum is weakly developed, barely visible dorsally. South Africa.....***R. amabala* sp. nov.**

– Basal body colour pattern is different; if the pronotum and T2 have large markings, these are yellow, and the basal body colour is brown or ferruginous (rarely, specimens of *R. aethiopica* may have yellowish markings or even reddish basal colour, but in these cases, the median scutellar carina is well developed dorsally) **35**

Nest. The nest is one of the most striking features of this species. In contrast to all previously known mainland African *Ropalidia* species, the only examined nest of this species was built directly on the tree trunk of a *Brachychiton* sp., in an area devoid of the surrounding lightly coloured grey lichen (Fig. 3a). The nest has the same colour as the lichen, suggesting that the nearby lichen fibres were used as the nest-building material, exhibiting a striking mimicry with the surroundings (Fig. 3b). There are additional reddish or blackish streaks in the cell wall; the opercula are below the outer cell margin, with traces of the cell wall (Fig. 3b). Notably, the marginal cells exhibit a fair degree of disordered building, failing to create a regular hexagonal form (Fig. 3b). After collection, the cell colour of the nest changed to mainly yellowish (Fig. 3c). The nest had 37 complete cells and about 20 incomplete marginal cells. Most of the cells were regular, but the marginal cells close to the lower edge of the nest were commonly irregular. There were 28 larvae in the nest and 24 detectable eggs; most of marginal cells had eggs laid in them, a single egg in each cell. The cocooned cells were unevenly distributed across the nest (Fig. 3b). The average cell wall width was 2.4±0.1 mm [n=15], while the average cell length of cells with cocoons was 11.1±1.5 mm [n=11]. The closed cocoons had a flattened surface that did not reach the outer cell margin. The cell paper is dense and brittle. In addition, there were four empty tachinid cocoons in the nest (Fig. 3c), suggesting a heavy tachinid parasitoid load. At the time of collection, in the early morning, there were 10 females and one adult male present on the nest.

Phylogenetic status. The new species was compared with three groups: (i) the mainland African *capensis*-group, (ii) non-capensis group and (iii) selected Malagasy *Ropalidia* species. The last group of species was selected on the basis of the nesting pattern, and it included three species that build the nests directly on tree trunks, in an area where the lichen or moss has been cleared. These include *R. minor* (de Saussure) [iNat: https://www.inaturalist.org/observations/69302879], with partly green nests, *R. saussurei* Kojima [iNat: https://www.inaturalist.org/observations/9669640, 85477179], with entirely green nests and *R. dubia* (de Saussure) [iNat: https://www.inaturalist.org/observations/81256863], with brownish nests in the lichen cleared area.

The comparison was based on three morphological features: the tarsal 1 spur on the foreleg in males (Fig. 4a), the tyloids of the terminal flagellomere in males, and the morphology of the propodeal excavation in both sexes.

The tarsal I spur was shown to be a character present in the *capensis* group of species (with two exceptions), while it is entirely lacking in the non-*capensis* group (Polašek et al. 2022).The same anatomical feature is present in males of all three analysed Malagasy

Figure 3. *R. amabala* sp. nov., nest **a** general appearance on a tree trunk **b** nest with wasps and closed cocoons **c** dried nest, with four tachinid cocoons.

species, but lacking in *R. amabala* sp. nov., suggesting that the newly described species is more closely related to the non-*capensis* group than either *capensis* or the Malagasy species.

The tyloids of the male antenna further support the closeness of *R. amabala* sp. nov. to the non-*capensis* group. The tyloids in *R. amabala* sp. nov. mostly resemble the mainland African species (most notably *R. nigrofemorata* Cameron), with a flattened surface that is not elevated above the flagellomere, especially in the terminal flagellomere, where the tyloid occupies most of the surface (Fig. 2c). In contrast, most Malagasy species, including all three examined species, have a thinner tyloid with a sharp inner margin on a substantially longer terminal flagellomere (Fig. 4c). Similar morphological characters are present in almost all members of the mainland *capensis* group (Polašek et al. 2022).

The third analysed character is the superior and inferior propodeal carina (Fig. 1c). Nearly all of the mainland non-*capensis* species have those developed, commonly as sharp cuticular structures (Fig. 1c), while these carinae are almost entirely lacking in the members of the *capensis* group. Furthermore, the analysed Malagasy species of *Ropalidia* do not have either the superior or the inferior carina developed (Fig. 4c).

The morphological characteristics of *R. amabala* sp. nov. exhibit the most similarity with the mainland *nigrofemorata* group of species, comprising *R. nigrofemorata* (Cameron), *R. tenebrica* Polašek and *R. tenuipilosa* Polašek, rendering this species a member of the *nigrofemorata* group. Among them, the nesting habits were only described for *R. tenuipilosa* Polašek, which constructs the nests on tree branches (iNat: https://www.inaturalist.org/observations/19815065). The comparison of the morphological characteristics of the member of the *nigrofemorata* group did not yield any additional reliable morphological difference.

Distribution. Eastern Cape and KwaZulu-Natal (South Africa).

Etymology. The name comes from the Zulu word *amabala*, meaning "spots", and refers to the six spots integrated with the posterior band on T2 and S2, characteristic for this species.

Figure 4. Comparative morphology of **a** *R. amabala* sp. nov., male, tarsal I spur **b** *R. saussurei* Kojima, male, tarsal I spur **c** *R. minor* (de Saussure), male, antenna **d** *R. saussurei* Kojima, propodeal excavation, oblique posterior view.

Discussion

The newly described African *Ropalidia* species exhibits similarity of the behavioural nesting pattern to some Malagasy species (Vesey-Fitzgerald 1950), but the morphological characteristics of both sexes suggest that this species is not evolutionarily closely related to the Malagasy lineage. Therefore, the nesting pattern described here is considered to have evolved independently from the Malagasy species. In addition, this is an example of a rare nesting architecture for mainland African *Ropalidia*. Besides using natural camouflage for concealment in the nest location, the whitish markings on the body, as opposed to more common yellow ones across the genus, also reflect the light greyish lichen colour's defensive mimicry.

Although there are no known mainland *Ropalidia* with a similar nesting pattern, there are comparable examples in a Malagasy species, most notably *Ropalidia dubia* (Vesey-Fitzgerald 1950). This species was reported to clear the lichen directly on the tree trunk and build a nest in the clearing, and hence the resultant nest was difficult to recognise. Notably, even the wasp behaviour reflected this tendency towards camouflage as a defence mechanism; instead of flying off from the nest if disturbed, the wasps "clung tenaciously to the comb and were quite difficult to drag off" (Vesey-Fitzgerald 1950). In addition, *Ropalidia cocoscola* Blommers has been reported to build nests in the cavities of the coconut palms stems (Blommers 2012), providing excellent visual (and physical) protection. Finally, numerous Malagasy *Ropalidia* species with mainly or entirely green(-yellow) colour (Blommers 2012), exhibit defensive mimicry through camouflage with their surroundings.

The selective pressure by ants is assumed to have been the primary evolutionary force driving the social wasp nest architecture (Jeanne 1975; Bouwma et al. 2007).

The ant-repelling properties of the nest stalk were not confirmed for *Ropalidia*, while they are common in *Polistes* (Jeanne 1975). Although such reports are not numerous, catastrophic ant predation of the entire *Ropalidia* colonies by *Dorylus* ants was recorded in Africa (iNat: https://www.inaturalist.org/observations/74875927), confirming the strong evolutionary pressure by ants. In contrast, the visually concealed nest and whitish-yellow body markings suggest that *R. amabala* sp. nov. is under strong selective pressure from visually driven predators. The same could be claimed for the numerous Malagasy *Ropalidia* species, suggesting that visually driven predation has an important role in the evolution of some of the African *Ropalidia*.

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